

DIETARY SELECTIVITY IN RELATION TO AVAILABILITY AND QUALITY OF FOOD FOR GOSLINGS OF CACKLING GEESE

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ABSTRACT.—Food selection by and diet of Cackling Goose (*Branta canadensis minima*) goslings were studied in relation to the quality and availability of food during brood rearing, 1977–1979. Arrowgrass (*Triglochin palustris*) was the most important food in the diet of goslings before wing-molt of adults and sometimes during molt. *Carex mackenziei* was the most common sedge in the diet but was less important than arrowgrass. Leaves of other species were relatively unimportant during premolt. Arrowgrass declined, while *Carex* seeds and crowberries (*Empetrum nigrum*) increased, in the diet as brood rearing progressed. Arrowgrass was highly preferred, whereas other sedges and grasses (except *C. mackenziei*) were avoided in areas for which both availability and consumption were measured. Preference for arrowgrass was related to its higher protein and energy content and lower cell-wall content compared to other forage species. Thus, geese benefitted nutritionally from selecting their preferred diet. Seeds and berries contained high levels of lipids and carbohydrates relative to green leaves. Less arrowgrass was consumed in a year when brood densities were higher than in the other 2 years of the study. Arrowgrass availability declined as brood rearing progressed in another year. Thus, Cackling Geese may have been reducing the availability of their most nutritious food, at least at high brood densities. Food quality in breeding areas may be influencing population dynamics of geese despite the high overall availability of green plants. Received 16 May 1983, accepted 7 November 1983.

GEESE are primarily herbivorous during the breeding season (Owen 1980: 127). Plant foods are generally lower in protein and energy content and are usually less digestible than animal foods. For geese, the relatively poor nutritional quality of green vegetation is exacerbated by their simple gastrointestinal tracts. Adult geese must replenish fat and protein reserves, which are at annual lows during hatching or early molt (Hanson 1962, Ankney and MacInnes 1978, Raveling 1979), and goslings must grow under these nutritional constraints. Nutrition during the brood-rearing period may affect such life history parameters as overwinter survival or future reproductive success. Poor food quality, in conjunction with the importance of nutrition following nesting, should have resulted in selection for foraging behavior that maximizes nutrient intake.

There have been few studies of the summer foraging ecology of geese that nest in the Arctic of North America other than general or food-habits investigations (Barry 1967, Mickelson 1975, Eisenhauer and Kirkpatrick 1977). Lief (1973) reported associations between preferred foraging areas and the presence of particular

plant species for both Lesser Snow Geese (*Chen caerulescens caerulescens*) and Canada Geese (*Branta canadensis*), and both he and Harwood (1975) demonstrated preferences for fertilized vegetation by grazing geese. None of these studies related the nutrient content of particular plant species to their importance in the diet, however. In view of the potential importance of summer foraging behavior, we undertook a study of this aspect of the ecology of Cackling Geese (*B. c. minima*) in order to describe their diet in relation to the availability and nutrient content of foods. The study was conducted from the first week of June through mid-August 1977–1979.

STUDY AREA

Our study area was located within the Clarence Rhode National Wildlife Range (now Yukon Delta National Wildlife Refuge) on the Yukon-Kuskokwim Delta, Alaska in the vicinity of the U.S. Fish and Wildlife Service field station at Old Chevak (61°N, 165°W). The primary study plot was a 40.4-ha area surrounding a cabin and observation tower between the Onumtuk slough and Kashunuk River (see Mickelson 1975 for further description).

We classified two main types of habitat on the study area: upland and lowland. Upland habitat consisted of relatively well-drained areas about 1.3–1.7 m above mean high-tide levels that were dominated by lichens, moss (*Sphagnum* spp.), *Empetrum nigrum*, *Rubus chamaemorus*, *Salix fuscescens*, and *Ledum palustre*. Areas about 0.5 m above mean high-tide levels were defined as lowland. About 50% of the lowland area consisted of small ponds (i.e. <0.8 ha in area). We recognized two subtypes of terrestrial lowland habitat, mudflat and meadow. Mudflats, adjacent to ponds, comprised 5% of terrestrial lowland habitat and were characterized by bare mud or small, nearly pure patches of either *Puccinellia phryganodes* or *Carex subspatheacea*, which were less than 5 cm tall. Nearly pure stands of *C. mackenziei* and *Hippuris tetraphylla* also occurred adjacent to ponds and mudflat areas. Meadows consisted of vegetation up to 20 cm in height, dominated by *C. rariflora*, *C. ramenskii*, *Calamagrostis deschampsoides*, and *Dupontia fisheri*. Scattered individuals of *C. mackenziei* occurred in both mudflats and meadows. *Triglochin palustris* (arrowgrass) occurred in small numbers in both lowland subhabitats and in stands of *C. mackenziei*.

METHODS

Plant species density.—Densities of plant species in meadows commonly used by wild geese were estimated by counting all individual shoots within a 14.5 cm² wire square, randomly placed 11 times along each of three 30-m-long transects (definition of individual shoot as in Chapin et al. 1980). Sampling locations along the transect line were selected before the first sampling date and were used for subsequent dates. Approximately the same transects were sampled three times during both 1978 and 1979, and the total numbers of individuals of each plant species at each sampling location (33 locations in each year) were recorded. We then calculated the mean percentage of total leaves contributed by each species. On mudflats, the wire square was tossed arbitrarily 62 times, and all arrowgrass individuals in the square were counted. The density of all other mudflat species combined was determined by counting all individuals within samples clipped from 15 0.1-m² quadrats during 1979.

Diet.—Goslings were removed from nests at hatching, imprinted on humans, and allowed to graze on the principal study area in both 1978 and 1979. The diet of these goslings was augmented with commercial poultry starter for their first 10 days. Imprinted goslings were periodically sacrificed after being allowed to feed in areas of known plant-species density. These feeding trials allowed a comparison between the abundance of plant species and their presence in the gosling diet. In addition, wild geese were collected by shooting on a 12.7-km² area adja-

cent to the principal study area during 1977, 1978, and 1979.

After all collections, esophageal contents were removed immediately, rinsed with 80% ethyl alcohol, and placed into vials. Within 3 h, esophageal samples were rinsed with water and returned to vials. Samples were refrigerated following rinsing and frozen within 24 h. Esophageal samples were sorted by plant species at the University of California, Davis, and freeze-dried to constant weight. Contributions of foods to the diet are reported as a percentage of dry weight.

Collection and chemical analysis of plant samples.—Mixed-species samples from mudflats and meadows, along with pure samples of *C. mackenziei* and *C. subspatheacea*, were collected for chemical analyses by clipping from 0.1-m² quadrats randomly placed within previously delineated 3 × 5-m plots during 1978 and 1979. These previously delineated plots were located in areas where grazing geese had been observed. Mixed-mudflat samples (nearly entirely *P. phryganodes*) included only erect shoots and leaves. Samples were clipped to litter level. Litter and standing dead material were removed in the laboratory and mixed-mudflat and *C. subspatheacea* samples were washed to remove excess mud. Individual arrowgrass plants were removed from mixed-meadow samples collected in 1978 to provide a pure sample of meadow arrowgrass for that year. All other arrowgrass samples were hand-collected.

All sampled plant species were represented in 1978 samples, whereas only *C. mackenziei*, mixed-mudflat, and arrowgrass were sampled in 1979. Plant samples were clipped on 25 June, on 3 and 4, 19, and 29 to 31 July, and on 7 August 1978, with the exception of early July mixed-mudflat samples, which were collected on 11 July 1978. All 1979 clipped samples were collected on 24 June, on 7, 17, and 28 July, and on 9 August. Samples of *T. palustris* were collected from mudflats and meadows on 10 dates through the summer of 1979. The amount of material was insufficient for separate analyses representing each date, however. Therefore five composite aliquots were formed for both mudflat and meadow *T. palustris* by combining material collected on the following pairs of dates: 24 and 30 June; 4 and 7, 17 and 21, 28 and 31 July; and 9 and 12 August. *Carex* seeds were collected only during August 1979, while *Empetrum nigrum* berries were collected on 7 and 29 July and 7 August 1978 and 9 August 1979.

Samples were frozen within 24 h. In Davis, samples were thawed, blotted lightly with paper towels, weighed, freeze-dried to constant weight, and then ground in a Wiley Mill to pass a 40-mesh sieve. Nitrogen was determined by the macro-Kjeldahl method (Horwitz 1975). Crude protein was estimated by multiplying 6.25 times Kjeldahl nitrogen. Crude fat was determined by extracting samples for 12 h with anhydrous ether in a Goldfish apparatus. Samples

were ashed by combustion of ether-extracted samples for 4 h at 500°C. Acid and neutral detergent-insoluble fractions (ADI and cell wall, respectively) were estimated by the Van Soest method (Goering and Van Soest 1970). Neutral detergent-insoluble material was saved, and the nitrogen content of this fraction was estimated by Kjeldahl analysis. Amino acid concentrations were determined on a Durham 500 amino-acid analyzer following 24 h hydrolysis in 6 N HCL (Spackman et al. 1958). Cysteine concentrations were determined using the same technique, except that samples were oxidized in performic acid for 24 h before hydrolysis (Hirs 1967).

Digestibility of protein in cell walls was calculated by assuming that the nonprotein fraction of cell walls was an indigestible marker (Drent et al. 1978). The percentage of protein in the cell-wall fraction of the diet was estimated by calculating a weighted average of the percentage of protein in the cell-wall fractions of the arrowgrass and nonarrowgrass portions of the diet, with the weights consisting of the proportional contributions of arrowgrass and non-arrowgrass foods to total cell wall in the diet. The protein content of cell walls in the feces was determined by Kjeldahl analysis of the fecal cell-wall fractions.

Statistical analyses.—Distribution of dietary data (percentage contribution to diet by a food) was non-normal and in some cases approached a bimodal distribution (see Fig. 1). For this reason we used Kruskal-Wallis or Mann-Whitney *U*-tests to compare the percentage contribution of a particular food to the diet of groups of goslings. Spearman rank correlation was used to analyze seasonal trends in diet and the correlation between cell-wall and protein content of plants. The dietary preference of imprinted goslings feeding in meadows was determined by means of a Mann-Whitney *U*-test to compare the percentage of leaves of a given type in esophagi versus that in the environment. We did not statistically evaluate the preference of imprinted goslings feeding on mudflats, because the use of different size quadrats for estimating densities of arrowgrasses and nonarrowgrasses precluded an estimation of among-sample variation of the percentage of arrowgrasses on mudflats. We analyzed the chemical constituents of plants by means of a 2-way ANOVA (species \times sampling dates, for protein and water) or 1-way ANOVA (other constituents) followed by a protected Least Significant Difference comparison between means (Carmer and Swanson 1973) in cases with a significant *F* value.

RESULTS

DIET

We divided the brood rearing period into three time periods for presentation of dietary data: preceding the molt of adult remiges (pre-

molt), coincident with the adult flightless period (molt), and coincident with fledging of young (fledging). The dividing points between premolt and molt collection periods were 14 July in 1979, 15 July in 1978, and 28 July in 1977. Molt and fledging periods were separated by 2 August in 1978, the only year in which collections were made during fledging. These periods correspond approximately to the following gosling ages: premolt, 1–23 days; molt, 24–41 days; fledging more than 42 days. Contributions of foods to the diet are expressed in aggregate percentages.

Imprinted and wild goslings differed significantly ($P < 0.05$) in diet in only 3 of 16 possible pairwise comparisons (4 food categories \times 2 yr \times 2 time periods within years, Fig. 1). These differences were due to the single collection during the 1979 molt period of three wild goslings from the same brood, which contained a significantly lower percentage of *T. palustris* and *C. mackenziei* and a significantly higher percentage of *Carex* seeds and *Empetrum* berries than did the tame goslings collected during the same period. There were no foods for which differences between the two groups in the consumption of a food were consistent between years. Because of the lack of differences between wild and tame goslings except for the one collection, we combined results from the two groups for subsequent analyses. (See Appendix for a complete summary of the diet of goslings.)

Because of initial difficulties in identification of plant species, some *C. subspathacea* was included with arrowgrass in the analysis of esophageal contents from goslings collected during 1977. Of the original arrowgrass sample from these goslings (a sample comprised of arrowgrass from all 1977 goslings that contained arrowgrass), 13% was available for reanalysis. *Carex subspathacea* comprised 4% of the dry weight of this material. This error did not have a substantial effect on either the presentation of, or the conclusions drawn from, our data.

Seasonal variation.—Arrowgrass predominated in the premolt diet of goslings, contributing 92% of the diet during this period in 1977, 44% in 1978, and 98% in 1979 (Fig. 1). Other foods were unimportant during premolt in 1977 and 1979, but *C. mackenziei* comprised 28% and other leaves (other *Carex* spp. leaves, grasses, and forbs) 19% of the 1978 premolt diet.

Arrowgrass declined in dietary importance

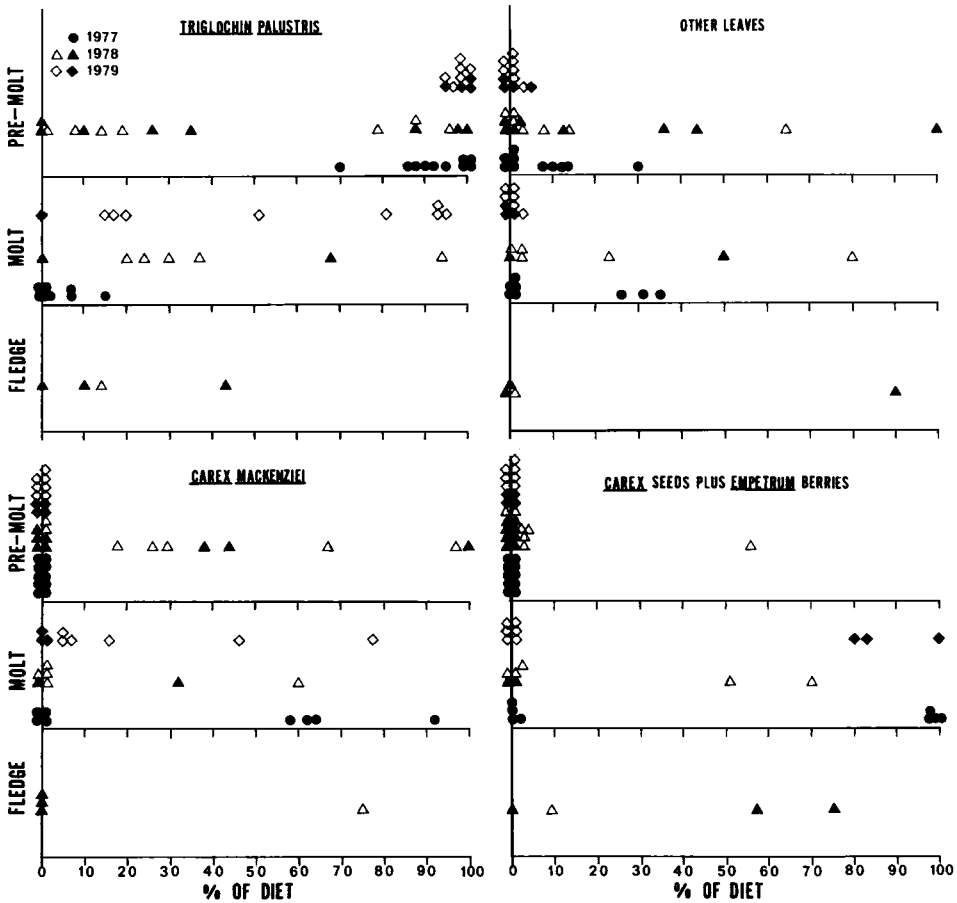


Fig. 1. Diet of Cackling Goose goslings during brood rearing 1977-1979. Each point within a food type corresponds to one individual, and each individual is represented in all four food types. Points are arrayed along the horizontal axis, representing percentage of diet (dry weight). Points representing goslings collected during the molt, premolt and fledging periods (see Results) are plotted separately within each food type. Points representing goslings collected in different years are separated vertically within plots for each of the three time periods. Open symbols represent tame goslings; solid symbols represent wild goslings.

during brood rearing in 1977 ($r_s = -0.71$, $P < 0.005$) and 1979 ($r_s = -0.77$, $P < 0.001$), while a slight nonsignificant negative trend was observed in 1978, the year of lowest premolt feeding on arrowgrass ($r_s = -0.19$, $0.2 < P < 0.4$, Fig. 1). *Carex* seeds and *Empetrum* berries tended to increase in the diet as brood rearing progressed in 1978 and 1979 ($r_s = 0.30$, $0.1 < P < 0.2$ and $r_s = 0.32$, $0.1 < P < 0.2$, respectively), and we observed a significant increase in 1977 ($r_s = 0.72$, $P < 0.001$).

Seasonal variation in the diet resulted in a reduction in the contribution of arrowgrass to 4% of the diet during molt in 1977, 39% in 1978,

and 52% in 1979 (Fig. 1), with a further reduction to 17% of the fledging diet in 1978. *Carex mackenziei* was the most important sedge in the diet during molt, comprising between 13% (1978) and 35% (1977) of the diet (18% in 1979). Seeds and berries increased from less than 10% of the premolt diet during all 3 yr to 49% of the molt diet in 1977, 18% in 1978, and 29% in 1979, and to 35% of the 1978 fledging diet. Other leaves combined comprised between 1% (1979) and 23% (1978) of the diet during molt (12% in 1977).

Among-year variation.—Goslings from the premolt period in 1978 contained significantly

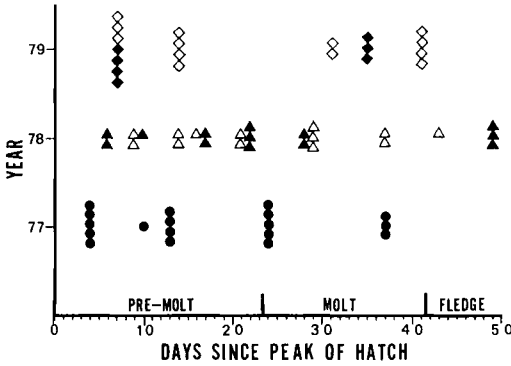


Fig. 2. Timing of collection of Cackling Goose goslings. Peak hatch was 4 July 1977, 21 June 1978, and 20 June 1979. Points from goslings collected within the same year are arrayed along the horizontal axis, while points from different years are segregated vertically. Each point represents one gosling. Open symbols represent tame goslings; solid symbols represent wild goslings.

less arrowgrass ($P < 0.002$) and significantly more *C. mackenziei* ($P < 0.001$) than did goslings from the same period in 1977 and 1979 (Fig. 1). Arrowgrass comprised a slightly (but nonsignificantly) larger fraction of the molt diet in 1979 than in 1978 and was a significantly larger fraction of the molt diet during these 2 yr than during 1977 ($P < 0.002$).

More goslings were collected later in the premolt period during 1978 than during 1977 and 1979 ($P < 0.01$, Fig. 2). This was probably not the cause of the among-year differences in premolt diet, however, for two reasons: (1) goslings from the first 14 days of the premolt period (in which all 3 yr were represented) still contained less arrowgrass in 1978 than in 1977 and 1979 ($P < 0.01$), and (2) goslings collected 15–16 days into the premolt period in 1978 (later than collections in 1977 and 1979) contained between 87% and 97% arrowgrass, among the highest levels recorded for 1978.

Preference.—Imprinted goslings were highly selective of arrowgrass leaves in meadows (Fig. 3, Mann-Whitney *U*-test, $P < 0.0002$), consuming them approximately five times more frequently than they occurred in the environment. Arrowgrass was selected at a similar relative rate on mudflats, although we could not evaluate this statistically, because we had no measure of variability in the availability of

arrowgrass on mudflats. Other sedges and grasses comprised a much smaller fraction of the diet than of available individuals.

CHEMICAL COMPOSITION OF VEGETATION

Concentrations of all constituents varied among species ($P < 0.001$, Tables 1, 2). Crude protein ($P < 0.0005$) and water content ($P < 0.01$) varied among sampling dates. Temporal variations in protein and water concentration were parallel among species (Kendall's Test of Concordance $P < 0.01$); the same proportion of each species' samples were collected on a given sampling date. We thus combined data across sampling dates for purposes of presentation. We will report on temporal variation in vegetation constituents in a separate paper.

Results dealing with the water content of vegetation must be interpreted with caution. Samples were collected under variable, but usually wet, conditions. Mixed-mudflat and *C. subspathacea* samples were washed to remove mud associated with these samples. As a result, the apparent water content of these samples was inflated and these data were not analyzed statistically.

Gross nutrients.—Crude protein content was highly variable among species and was highest (30%) in arrowgrass from mudflats (Table 1). Crude protein in arrowgrass from meadows and in *C. subspathacea* averaged 19%, whereas all other types of green vegetation and *Carex* seeds contained between 13.3% and 15% protein. *Empetrum nigrum* berries contained substantially less protein (5%) than did other foods.

Crude fat concentrations were 2–3 times greater in seeds and berries (7.8–9.7%) than in green plants (3.2–4.4%, Table 1). The ash content of seeds and berries (2.4–3.9%) was considerably lower than that of vegetative parts of green plants (6.1–13%, Table 1).

Cell wall.—Arrowgrass contained substantially less cell wall than other green plants, and there was lower cell-wall content in arrowgrass from mudflats than arrowgrass from meadows (Table 2). *Carex subspathacea*, *C. mackenziei*, and mixed-mudflat vegetation did not differ from one another in percentage cell wall. Cell walls constituted the largest proportion (58.3%) of dry weight (among green plants) in mixed-meadow vegetation.

Mean levels of ADI (consisting of cellulose, lignin, and some ash) varied between 21.1% and

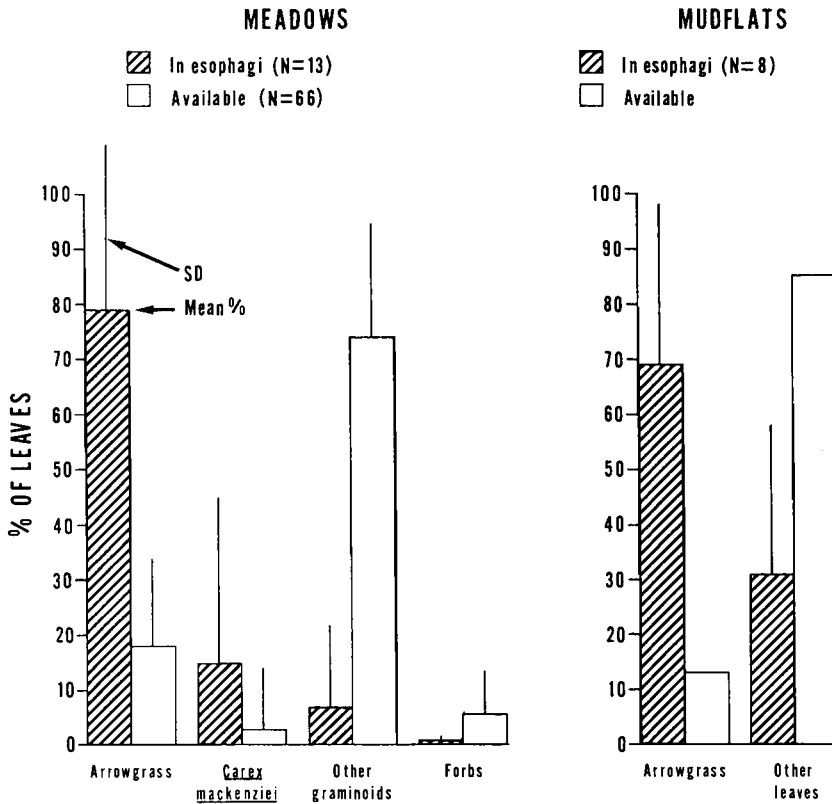


Fig. 3. Dietary selectivity by imprinted goslings in 1978 and 1979. Species composition of leaves in esophagi was determined by counting all leaves in esophagi of goslings that had fed in the vicinity of meadow vegetation transects (13 goslings) or on mudflats (8 goslings). We did not present variability in percentage of leaves available on mudflats, because numbers of arrowgrass leaves were estimated from quadrats of a size different from those for other leaves (see Methods).

29.2% of plant dry weights (Table 2). *Carex mackenziei* and *C. subspathacea* contained significantly less ADI than mixed-meadow vegetation, whereas mixed-mudflat vegetation contained intermediate levels of ADI. Other samples were not compared statistically due to insufficient sample sizes.

Significant differences among species in the percentage of cell wall comprised of protein were not detected (1-way ANOVA, $P > 0.05$, Table 2). When averaged across all species, cell walls contained 0.72% nitrogen, or 4.5% crude protein. This is a slight underestimate, because cell-wall fractions were contaminated with cellite from the NDF procedure. The percentage of cell wall was inversely correlated with total crude protein ($r_s = -0.32$, $P < 0.01$). In conjunction with the constant protein fraction in

cell walls, this resulted in a larger fraction of total protein being associated with cell walls in plants that contained less total protein. Cell-wall protein constituted 2–4% of total crude protein in arrowgrasses but 22% of crude protein in mixed-meadow vegetation.

Available protein and carbohydrate.—Protein associated with cell walls is relatively unavailable to nonruminants (Van Soest and Moore 1965). Cackling Geese digested approximately 38% of cell-wall protein (Sedinger and Raveling unpubl. data). Hence, the association of protein with cell walls significantly reduced the protein available for digestion. Available protein was further reduced below crude protein, because the 6.25 multiplier used to calculate crude protein failed to account for nonamino-acid nitrogen in plants (McDonald et al. 1973).

TABLE 1. Nutrient content of foods used by Cackling Geese ($\bar{x} \pm SE$).

Plant species/ type	H ₂ O (%)	Crude protein ^a (%)	Crude fat ^a (%)	Ash ^a (%)
Arrowgrass (from mudflats)	86.5 \pm 1.5 (A) ^b (n ^c = 5)	30.1 \pm 1.7 (A) (n = 5)	3.8 ^{NT} (n = 1)	13.0 ^{NT} (n = 1)
Arrowgrass (from meadows)	84.9 \pm 0.7 (A) (n = 5)	19.5 \pm 1.5 (B) (n = 10)	3.9 ^{NT} (n = 1)	12.5 ^{NT} (n = 1)
<i>Carex subspathacea</i>	79.6 \pm 1.7 ^{NT} (n = 5)	19.0 \pm 1.6 (B, C) (n = 5)	4.4 \pm 0.4 (A) (n = 5)	9.2 \pm 1.0 (A) (n = 5)
<i>C. mackenziei</i>	78.3 \pm 1.1 (B) (n = 15)	14.0 \pm 0.7 (D, E) (n = 15)	3.2 \pm 0.2 (A) (n = 13)	9.2 \pm 0.4 (A) (n = 13)
Mudflat-mixed	82.2 \pm 0.6 ^{NT} (n = 20)	15.2 \pm 0.6 (C, D) (n = 20)	3.2 \pm 0.2 (A) (n = 17)	7.9 \pm 0.7 (A) (n = 15)
Meadow-mixed	70.1 \pm 1.0 (C) (n = 15)	13.3 \pm 0.6 (E) (n = 15)	3.2 \pm 0.1 (A) (n = 15)	6.1 \pm 0.1 (B) (n = 15)
<i>C. rariflora</i> seeds	66.1 ^{NT} (n = 1)	14.9 ^{NT} (n = 1)	7.8 ^{NT} (n = 1)	3.9 ^{NT} (n = 1)
<i>Empetrum nigrum</i> berries	80.9 \pm 1.8 (A, B) (n = 4)	5.0 \pm 0.4 (F) (n = 4)	9.7 ^{NT} (8.7-10.6) ^d (n = 2)	2.4 ^{NT} (2.2-2.6) (n = 2)

^a Percentage of dry weight.

^b Entries within a column, not sharing a common capital letter were significantly different ($\alpha = 0.05$). NT indicates entry was not tested (because of small samples or bias in water content data; see text).

^c n = number of samples from distinct sampling dates and/or areas.

^d Parentheses indicate range for crude fat and ash of *E. nigrum* berries.

TABLE 2. Cell-wall content (% dry weight) of food plants used by Cackling Geese ($\bar{x} \pm SE$).

Plant species/type	Neutral detergent insoluble (% cell wall)	Acid detergent insoluble (%)	Cell-wall nitrogen ^a (%)
Arrowgrass (mudflat)	23.7 \pm 1.2 (A) ^b (n ^d = 4)	23.7 ^{NT} (n = 1)	0.4 (0.3-0.4) ^c (n = 2)
Arrowgrass (meadow)	29.1 \pm 0.8 (B) (n = 5)	28.0 (24.0-32.0) ^{NT} (n = 2)	0.5 \pm 0.1 (n = 4)
<i>Carex subspathacea</i>	47.6 \pm 1.6 (C) (n = 5)	23.1 \pm 0.9 (A, B) (n = 5)	0.8 (0.7-1.0) (n = 2)
<i>C. mackenziei</i>	50.4 \pm 0.8 (C) (n = 15)	21.1 \pm 0.8 (A) (n = 15)	0.8 \pm 0.1 (n = 5)
Mudflat-mixed	49.5 \pm 1.9 (C) (n = 20)	25.8 \pm 1.0 (B, C) (n = 20)	0.9 \pm 0.2 (n = 3)
Meadow-mixed	58.3 \pm 1.0 (D) (n = 15)	27.1 \pm 0.4 (C) (n = 15)	0.8 \pm 0.1 (n = 4)
<i>C. rariflora</i> seeds	60.4 ^{NT} (n = 1)	22.7 ^{NT} (n = 1)	—
<i>Empetrum nigrum</i> berries	36.8 ^{NT} (n = 1)	29.2 ^{NT} (n = 1)	—

^a No significant, among-species variation (1-way ANOVA, $P > 0.05$).

^b Entries within a column not sharing a common capital letter were significantly different ($\alpha = 0.05$). NT indicates entry was not tested.

^c Values in parentheses are the range for entries when n = 2.

^d n = number of samples from distinct sampling dates and/or areas.

TABLE 3. Available protein and carbohydrate content of foods used by Cackling Geese (% dry weight).

Plant species/type	Available protein ^a (%)	Soluble carbohydrate ^b (%)
Arrowgrass (from mudflats)	24.3	35.4
Arrowgrass (from meadows)	15.0	39.8
<i>Carex subspathacea</i>	13.7	25.9
<i>C. mackenziei</i>	9.4	28.7
Mudflat-mixed	10.4	29.8
Meadow-mixed	8.5	24.5
<i>C. rariflora</i> seeds	11.3	17.6
<i>Empetrum nigrum</i> berries	3.3	48.4

^a Calculated from: % available protein = $5.44 \cdot \% N - 1.47 - 0.62 \cdot \% \text{ protein in cell walls}$. For seeds and berries % available protein = $5.44 \cdot \% N - 0.62 \cdot \% \text{ protein in cell walls}$ (because seeds and berries contained little nonprotein nitrogen).

^b Percentage soluble carbohydrate = $100\% - \% \text{ cell wall} - \% \text{ non-cell-wall protein} - \% \text{ crude fat} - \% \text{ ash}$. % non-cell-wall protein = $5.44 \cdot \% N - 1.47 - \% \text{ protein in cell walls}$ (except seeds and berries; see a).

We estimated the true relationship between nitrogen and protein by regressing the sum of the percentages of amino-acid concentrations (Sedinger in press) against the percentage of nitrogen, using nine samples of green vegetation. The accurate relationship between protein and nitrogen was:

$$\begin{aligned} \text{percentage of} \\ \text{true protein} &= -1.47 + 5.44 \\ &(\text{percentage of} \\ &\text{nitrogen}). \end{aligned}$$

Accounting for cell-wall protein and the conversion from Kjeldahl nitrogen to protein resulted in estimates of protein available for digestion of between 19% (arrowgrass) and 36% (mixed-meadow) below crude protein values (Table 3).

Soluble carbohydrate comprised 48% of *Empetrum nigrum* berries (Table 3), whereas arrowgrass contained the largest fraction of soluble carbohydrate among green plants (35.4–39.8%). Other green plants contained between 24.5% (mixed-meadow) and 29.8% (mixed-mudflat) soluble carbohydrate.

DISCUSSION

Diet.—Arrowgrass dominated the summer diet of young Cackling Geese before they fledged despite its low abundance relative to

other graminoid species. Such selectivity resulted both from preferential foraging in mudflats (Sedinger and Raveling unpubl.), where arrowgrasses were more available, and from discrimination among available food plants at particular feeding sites (Fig. 3). The preference for arrowgrass displayed by Cackling Geese means that actual food availability was much lower than one might qualitatively assume from the large extent of sedge meadows on the Yukon-Kuskokwim Delta.

The preference for arrowgrass was associated with its content of protein, water, ash, and soluble carbohydrate being higher than, and its cell-wall content being lower than, that of other graminoids. The relationship between available nutrients and food preference was highlighted by a preference for foraging in mudflats (Sedinger and Raveling unpubl.), where arrowgrass contained more protein and less cell wall than it did in meadows. The choice among grasses and sedges was less clearly related to nutrient content. *Carex subspathacea* contained the highest protein and lowest cell-wall content among grasses and sedges; yet, it was not an important component of the diet. *Carex mackenziei* was consumed at 2–3 times the rate of other grasses and sedges combined; yet, it did not contain higher protein or lower cell-wall content than these other species. *Carex mackenziei* contained less ADI than either mudflat or meadow vegetation. Less cellulose and lignin in cell walls of *C. mackenziei* may have allowed greater mechanical breakdown of plant cell walls, thus rendering nutrients in this species more available and making it a preferred food. Acid and neutral detergent fiber contents of diets were both negatively correlated with growth rates of meadow voles (*Microtus pennsylvanicus*), herbivores with simple gastrointestinal tracts, indicating that cellulose and/or lignin interfered with utilization of nutrients (Russo et al. 1981).

The lack of correspondence between nutrient content and contribution to the diet of foods other than arrowgrass may have been partially due to differences between the chemical composition of vegetation actually consumed by geese and vegetation samples collected for chemical analysis. Arrowgrass from esophageal contents of geese contained an average of 28% and *C. mackenziei* leaves 51% more protein than did hand-collected or clipped leaves of the same species (Sedinger and Rav-

eling unpubl. data). An unknown fraction of this "extra" protein was due to contamination by saliva (Moss 1972), but higher protein levels in esophageal samples were probably at least partially due to selection by geese of higher-quality feeding areas or higher-quality plants or plant parts. Geese have the ability to select plants with higher protein content (Lieff et al. 1970, Harwood 1975, Owen et al. 1977). Geese also select younger and probably more nutritious leaves from within plants (Prins et al. 1980), and McLandress and Raveling (1981a, b) demonstrated that geese grazed in a manner that maximized nutrient intake. If Cackling Geese were capable of detecting patches of vegetation of higher nutrient content, then species that were more variable in nutrient content (e.g. *C. mackenziei*) could have been preferred due to the presence of some plants or plant parts with high nutrient content, even though there were no between-species differences in mean nutrient content in our samples or in the species as a whole.

Carex subspathacea and *P. phryganodes* had low growth forms in which arrowgrass was readily available. Hence, on mudflats, geese were able to maintain a high rate of intake while feeding exclusively on arrowgrass. Arrowgrass was probably less available in stands of *C. mackenziei* due to the longer growth form of the latter species. This could have resulted in *C. mackenziei* being grazed along with arrowgrass in order to increase the rate of intake over what would have been possible if only arrowgrass were being eaten. Thus, *C. subspathacea* and *P. phryganodes* were probably consumed less frequently than expected, because their growth forms allowed a high enough rate of intake of arrowgrass alone, whereas *C. mackenziei* was consumed more frequently than expected from its nutrient content, because its growth form precluded a high enough rate of intake when feeding on arrowgrass alone.

The minimal contribution of invertebrates to the diet (Appendix; Mickelson 1973) is of interest, because such foods provide a concentrated source of protein of high biological value (Krapu and Swanson 1975) known to be important in the early diet of other waterfowl (Sugden 1973). Goslings of Cackling Geese readily consumed insects under enclosed conditions (pers. obs.). A relatively small return from consuming single insects at a time in meadows may select against the consumption

of insects except under conditions (e.g. cold weather, M. R. McLandress pers. comm.) in which insects are highly vulnerable and thus available in large numbers. The grazing behavior of geese may also contribute, because search images required for correct selection of preferred food plants may preclude feeding on insects except when superabundant and available.

Nutritional considerations.—Discrimination among potential foods resulted in a clear nutritional benefit to Cackling Geese. If the ability of geese to select more nutritious individuals from within a species is disregarded and only the nutritional advantage of selection among species is considered, the protein content of the actual diet was 37% higher in meadows and 43% higher in mudflats than random selection would have provided. Dietary protein was directly related to the growth rate of domestic and Mallard (*Anas platyrhynchos*) ducklings (Dean 1972, Street 1978). Adult muscle size may be maximized by sufficient dietary protein during early development (Moss et al. 1964, Swatland 1977). Canada Goose goslings grew faster when raised on fertilized vegetation than on unfertilized vegetation (Lieff 1973) and goslings of Bar-headed Geese (*Anser indicus*) grew faster on an artificial diet than they did in the wild (Wurdinger 1975), indicating that diet in the wild was inadequate for maximum rate of growth.

A preference for arrowgrass also increased energy content in the diet because of its higher soluble carbohydrate levels compared to grasses or sedges. Low energy levels in the diet of chicks less than 10 days old may result in both fewer and smaller adipose cells (March and Hansen 1977). Hence, the dietary selectivity displayed by Cackling Geese probably maximized growth rate, final adult body size, and ability to store both fat and protein. These factors could significantly influence their reproductive capacity as adults (Ankney and MacInnes 1978, Raveling 1979). Faster growth may also have reduced susceptibility to predation, and, as Scott et al. (1955) demonstrated, mortality due to cold and wet weather may be reduced by improvement of the diet in gallinaeous birds. Furthermore, Cole (1979) found that larger Lesser Snow Goose goslings survived better than smaller ones in cool summers.

Seasonal and annual variation in diet.—Cackling

Geese ingested less arrowgrass and more energy-rich *Carex* seeds and *Empetrum* berries as summer progressed. This change in diet was possibly in response to an increased requirement for energy to allow premigratory fat deposition and to a decreased growth demand. Reduced arrowgrass consumption, however, began while goslings were still growing rapidly and presumably still requiring a high-protein diet. Esophagi of four imprinted goslings collected on 31 July 1979, approximately 1 week before fledging, contained between 81% and 95% arrowgrass, indicating that this food was readily consumed when available, even during the late brood-rearing period. Biomass of arrowgrass declined in mid-July 1979 (Sedinger and Raveling unpub. data) on mudflats, indicating that declining consumption of arrowgrass was at least partially due to reduced availability of that species.

Arrowgrass comprised a smaller fraction of both the premolt and molt diets during 1978 than during 1979 (Fig. 1), although the difference was significant only during premolt ($P < 0.002$). This was associated with higher densities of geese on our principal study plot during 1978 than during 1979 [an average of 23 Cackling Goose families during 1978 vs. 12 families during 1979 and an average of 1 family of either Brant or Emperor Geese (*Chen canagica*) in each year]. This inverse correlation between goose density and the presence of arrowgrass in the diet, in conjunction with declining arrowgrass biomass through the brood-rearing period, indicates that Cackling Geese were reducing the availability of their preferred food, especially when densities of geese were high. Reduced consumption of arrowgrasses due to reduced availability would reduce protein and energy intake by geese.

Population and distribution considerations.—To the extent that nutrition influences survival and future reproduction, availability of vegetation of sufficient quality may, in conjunction with habitat features providing for safety from predation, determine preferred nesting habitat. Nesting geese are not uniformly distributed throughout arctic areas, and their distribution may be related to the presence of brood-rearing areas with the "proper" plant species composition. Lieff (1973) suggested that different nesting and brood-rearing areas at McConnell River, N.W.T., Canada produced different "quality" goslings, which may have been re-

lated to differences in food quality. In view of the ongoing commercial development of arctic areas, it is important to determine the contribution of particular plant species to the maintenance of goose populations and to determine the relationship between these plant species and preferred goose breeding areas.

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APPENDIX. Food of Cackling Goose goslings on the Yukon-Kuskokwim Delta. Results from 64 goslings containing a total of 14.6 g in esophagi (dry weight).

Food species	Frequency of occurrence	Dry weight (%)
<i>Triglochin palustris</i>	88	68
<i>Carex mackenziei</i> leaves	38	18
<i>C. ramenskii</i> leaves	20	1
<i>C. rariflora</i> leaves	5	Trace*
<i>C. subspathacea</i> leaves	2	Trace
<i>C. glareosa</i> leaves	6	Trace
<i>Carex</i> (unident.) leaves	5	Trace
<i>Puccinellia phryganodes</i> leaves	6	1
<i>Graminae</i> (unident.) leaves	14	Trace
<i>Hippuris tetraphylla</i> leaves	11	Trace
<i>Potentilla egedii</i> leaves	8	Trace
<i>Empetrum nigrum</i> leaves	6	Trace
<i>Stellaria crassifolia</i> leaves	11	Trace
<i>Ranunculus hyperborea</i> leaves	5	Trace
<i>Chrysanthamum arcticum</i> leaves	2	Trace
<i>Salix ovalifolia</i> leaves	2	Trace
<i>Carex</i> seeds	28	8
<i>E. nigrum</i> seeds	6	1
<i>E. nigrum</i> berries	3	1
Moss (unident.)	2	Trace
Litter	14	Trace
Insects	16	Trace

* Trace = <1%.

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